

Maximum Walking Speed and Lower Limb Length in Hominids

DAVID WEBB

Department of Anthropology / Sociology, Kutztown University, Kutztown, Pennsylvania, 19530

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ABSTRACT In 1984, Helene (Am. J. Physics 52:656) and Alexander (Am. Scientist 72:348-354) presented equations which purported to explain how lower limb length limited maximum walking speed in humans. The equations were based on a simplified model of human walking in which the center of mass (CoM) "vaults" over the supporting leg. Increasing walking speed by increasing stride frequency or stride length would increase the upward acceleration of the CoM in the first half of stance phase, to the point that it would be greater than the downward pull of gravity, and the individual would become airborne. This constitutes running by most definitions.

While these models ignored various mechanical factors, such as knee flexion during midstance, that reduce the vertical movement of the CoM, the general idea is plausible inasmuch as the CoM of the body does oscillate vertically with each step. One hypothesis tested here is whether it is indeed the interaction between the pull of gravity and the individual's own upward acceleration that determines at what speed (or cadence) he changes from walking to running.

Another hypothesis considered is that increased lower limb length (L) was selected for in early hominids, because of the locomotor advantages of longer lower limbs. Results indicate, however, that while L was clearly related to maximum possible walking speed, it was not an important factor in determining maximum "comfortable" walking speed. These and other results from the recent literature suggest that increased lower limb length provided no selective advantage in locomotion, and other explanations should be sought. © 1996 Wiley-Liss, Inc.

DERIVATION OF HYPOTHESES

We may make the informal observations that longer-legged individuals tend to walk faster than those with shorter legs. Also, we may note that those with longer legs apparently attain a greater maximum walking speed than those with shorter legs. But, is this really true, and if so what is the specific relationship between lower limb length and walking speed? And what can this tell us about the selection for longer lower limbs during hominid evolution?

There are at least two ways of defining maximum walking speed: maximum possible speed (V_{\max}) and maximum comfortable

speed (V_{comf}). Two questions then arise: *can* those with longer lower limbs walk more quickly and, just as importantly, *do* they walk more quickly?

Maximum running speed has been shown to be significantly correlated ($r^2 = 18.1\%$) with hindlimb length in cursorial mammals (Garland and Janis, 1993). In addition, the change from walking to running in animals may also be related to the animals' limb length (Alexander, 1984a). These suggest the possibility that V_{\max} is related to lower limb length (L) in bipedal hominids, as well.

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Alexander (1984a) suggested that V_{\max} and maximum comfortable walking speed, V_{conf} , are both related to limb length in many animals, including humans. On the other hand, Cavagna and Kaneko (1977) have shown that V_{conf} in humans may be determined mostly by energy efficiency. That is, when walking very quickly, we will change to running when a unit increase in speed would cost more if we walk faster than if we run. Hoyt and Taylor (1981) came to similar conclusions about gait changes in horses. However, these last two studies were based on empirical data which did not include limb measurements, and hence could not easily be applied to fossil hominids. From Cavagna and Kaneko's (1977) study, we would expect longer-legged individuals to walk more quickly only if they possess a greater speed of maximum efficiency, or are more efficient at greater speeds, than shorter-legged people. However, this assumption of a correlation between limb length and speed/efficiency may not be valid (Steudel, 1996). If the assumption is incorrect, we cannot expect a significant correlation between lower limb length (L) and maximum comfortable walking speed (V_{conf}).

Hypotheses

Cappozzo (1982) has noted that "as walking speed augments, the vertical acceleration amplitude spectrum increases in magnitude and shifts towards frequencies where body organs are known to undergo resonance." On that basis, he suggested that the strain on body tissues may be a limiting factor on maximum walking speed, or more precisely, on maximum cadence. Cadence has been shown by many authors to be related to speed in a relatively simple manner when individuals are considered singly (see, for example, Cappozzo, 1982; Inman et al., 1981; Herman et al., 1976). However, when comparing cadence and speed among several subjects, lower limb length becomes an important factor (Webb, 1989; Alexander, 1984a; Charteris et al., 1981; Grieve and Gear, 1966).

Gravity-based hypotheses

Alexander (1984b) and Helene (1984) provide models which predict the maximum

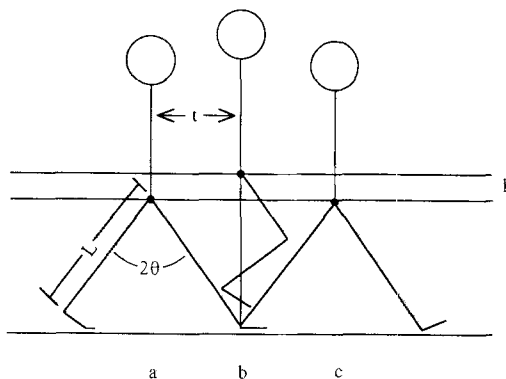


Fig. 1. Schematic diagram of walking subject showing (a) first heel strike, (b) mid-stance, and (c) next heel strike. The amount of vertical oscillation of the CoM is h ; lower limb length is L ; the maximum angle (at heel strike) from knee to hip to opposite knee is 2θ ; the time from heel strike to mid-stance is t .

walking speed of a human based on lower limb length. Both are based on the effects of gravity on the center of mass (CoM) of the body as it vaults over the supporting limb as in Figure 1. Alexander (1984b) uses the following equation as a practical limit on walking speed:

$$v \leq \sqrt{gL} \quad (1)$$

where v is walking speed, g is the acceleration due to gravity and L is lower limb length. His justification for this is that the acceleration of the CoM towards the ground at mid-stance is equal to v^2/L , if the CoM travels in a circular arc over the supporting limb. Since this acceleration must not exceed the downward pull of gravity (lest the individual become airborne), v^2/L cannot exceed g , and with the appropriate algebraic transformation we arrive at Equation 1. Because g is a constant, we can rewrite the formula for maximum walking speed (V_{\max}) as

$$V_{\max} \propto \sqrt{L}. \quad (2)$$

Helene (1984) developed a similar but more complex equation to describe the relationship between walking speed and lower limb length:

$$v = L \sin \theta \sqrt{g/2h} \quad (3)$$

where $L \sin \theta$ is the forward distance from heel strike to mid-stance (or mid-stance to next heel strike), and $\sqrt{g/2h}$ is the time required to move that distance. In this case, h is the vertical displacement of the CoM during each step. Helene (1984) arrived at these values by assuming that the time (t) for each step could be divided into two approximately equal segments, one for raising the CoM during the first half of stance phase (heel strike to mid-stance) and the other for letting the CoM fall under gravity during the second half (mid-stance to next heel strike). The duration of the second half would be limited by the acceleration due to gravity. Using the well-known formula for distance travelled in a certain time under a given acceleration, $d = \frac{1}{2} at^2$, where in this case $d = h$ and $a = g$ (9.8 m/sec^2), algebraic manipulation provides the time for each half of stance phase, $t = \sqrt{2/hg}$. Speed, defined as distance travelled per unit time, becomes

$$v = \frac{L \sin \theta}{\sqrt{2h/g}} \quad (4)$$

which reduces to Equation 3.

If we then assume, as Alexander (1984b), that the CoM vaults in a circular arc over a straight lower limb, h can be described in terms of θ and L , specifically $h = L - L \cos \theta = L(1 - \cos \theta)$, as in Figure 2. [In fact, h is slightly less than expected due to several "determinants of gait" which tend to reduce vertical displacement of the CoM (Saunders et al., 1953).] Helene (1984) assumed that θ would be fairly constant among individuals, making $(1 - \cos \theta)$ and $\sin \theta$ constants. Since the limiting factor, g , is a constant, this reduces Equation 4 to

$$v \leq \frac{L k_1}{\sqrt{L} k_2} \quad (5)$$

and once again we are left with

$$V_{\max} \propto \sqrt{L}. \quad (5)$$

Evidence from the literature suggests that gravity is indeed a limiting factor on maximum walking speed. Bhattacharya et al.

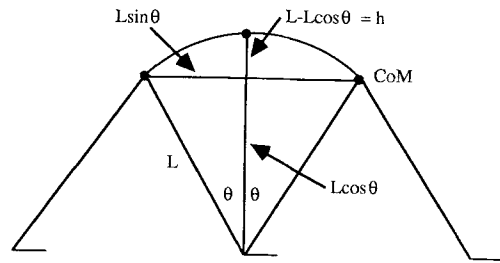


Fig. 2. Detailed schematic of lower limbs and CoM during one step, showing derivation of various estimated kinematic variables.

(1980) showed that the peak upward acceleration of the lower backs and foreheads of eight subjects, walking at 4.8 km/h (3.0 mph) averaged 0.9g and 0.8g, for back and head, respectively. However, while running at 8.1 km/h (5.0 mph), the accelerations were about 3.7g and 2.6g for back and head, respectively (Bhattacharya et al., 1980). Comparable values were measured by Dupuis et al. (1976), who found that the peak vertical acceleration of the head while walking on a road was 8.4 m/sec² (0.86g), and 35.8 m/sec² (3.7g) while running. Even Cappozzo (1982), who suggested the resonance-based hypothesis above, noted that the maximum upward accelerations of the head, shoulders and pelvis did not exceed the pull of gravity, even at high walking speeds like 2.31 m/sec (5.17 mph). Hence, while walking, peak upward acceleration is less than gravity and, while running, it is more.

Simplifying assumptions

In order to produce useful models, both Alexander (1984b) and Helene (1984) have made a number of simplifications to the true movement of the human body during walking. The most important are as follows:

- knee does not flex during stance phase
- contralateral hip does not drop during stance phase
- hip rotation in the horizontal plane does not occur
- ankle is extended negligibly at heel strike
- ankle flexes negligibly at toe-off
- individuals do not differ significantly in

- inter-knee angle (thigh extension and flexion) when walking near maximum speed
- difficulty of oscillating lower limbs in the sagittal plane is not a limiting factor on cadence
- differing energy costs at different speeds and gaits are unimportant
- elasticity of tissues and hence storage of elastic energy are negligible
- upper limbs do not significantly affect the vertical movement of the CoM.

Only by accepting these simplifying assumptions can we develop a relatively simple mathematical model.

Application to fossils

A series of hominid femora (Table 1) was used to indicate how lower limb length has evolved over the past 4 Ma. Femoral length was used, because a relatively large number (36) of fossil and recent femora were available. It must be recognized that this can show us only an approximation of the trend in lower limb evolution, since the relative length of the tibia may have changed over time. Hence, the relationship between femur length and lower limb length may also have changed as tibia length changed, even if femur length remained constant. A change in relative tibia length (crural index) is in fact suggested by Vancata (1991), but the number of associated femora and tibiae is small, making estimates of crural index unreliable, and the change was a decrease in crural index by only 2% from *Australopithecus afarensis* to *Homo habilis* (Vancata, 1991).

Figures 3 and 4 demonstrate the evolution of femur length over the past 4 Ma. Note that femur length, and therefore probably lower limb length, increased rapidly during the first 2 Ma, then changed little thereafter, as suggested by McHenry (1991).

If the gravity-based hypothesis is true, it provides a partial explanation for this trend, since it suggests that the advantages of longer lower limbs are reduced as the limbs get longer. In other words, because V_{\max} is proportional to $\sqrt{g/2h}$, shorter-legged hominids will gain more per unit increase in limb length than longer-legged hominids. If maxi-

mum walking speed is correlated with greater efficiency at a given sub-maximum speed, this would have given a greater selective advantage for longer legs in early hominid evolution than in later hominid evolution. There may, therefore, have come a time when the advantages of growing longer lower limbs were outweighed by the disadvantages (e.g., the metabolic costs of maintaining larger body mass or increased joint forces especially during running). This would have occurred earlier in hominid evolution if the gravity-based hypothesis is true than if a simple linear relationship between L and V_{\max} applies. Hence, the gravity-based hypothesis may be part of a self-limiting process.

As in Alexander's (1984a) paper, an important assumption has been made here: maximum comfortable walking speed, V_{comf} , must be related to L in a positive fashion, as is hypothetically the case for V_{\max} . Maximum comfortable walking speed appears to be related to energy efficiency, in humans (Cavagna and Kaneko, 1977) and some other mammals (Hoyt and Taylor, 1981); and hence, if energy efficiency at a given speed is positively correlated with lower limb length, then natural selection would have favored longer lower limbs in hominids, over the past 4 Ma. However, recent work by Steudel (1996; Steudel and Beattie, 1995, 1994) has shown that this is not the case, at least for 21 species of mammals. A review of data available from the literature suggested that this is probably also true of humans, although the range of L and the number of subjects were rather small in the articles cited by Steudel (1996). A more thorough test of this assumption is therefore warranted, if the results of the gravity-based hypothesis are to be applied to fossil hominids.

Testable hypotheses

The null hypothesis can be stated as one deriving from the initial, informal observation that longer-legged people can walk faster than shorter-legged ones, and from Garland and Janis' (1993) work relating limb length to maximum running speed in quadrupeds (both variables corrected for body mass). Hence, $H_0: V_{\max} \propto L$. If H_0 is true, then L will be a better predictor of V_{\max} than \sqrt{L} will, and a log-log regression of V_{\max} on

TABLE 1. Hominid femoral specimens with their approximate dates and measured or estimated lengths

Specimen(s)	Time (Ma)	Femur (m)	Source(s)	Taxon
AL 288-1	-3.1	.280	McHenry ^{1,2}	<i>A. afarensis</i>
AL 333-3	-3.1	.404	McHenry ^{1,2}	<i>A. afarensis</i>
AL 333-4	-3.0	.340	Day ¹ ; Vancata ²	<i>A. afarensis</i>
AL 129-1	-3.0	.285	Day ¹ ; Vancata ²	<i>A. afarensis</i>
Sts 14	-2.6	.295	McHenry ^{1,2}	<i>A. africanus</i>
Stw 25	-2.6	.320	McHenry ^{1,2}	<i>A. africanus</i>
Stw 99	-2.6	.380	McHenry ^{1,2}	<i>A. africanus</i>
Sts392	-2.6	.311	McHenry ^{1,2}	<i>A. africanus</i>
Stw 443	-2.6	.359	McHenry ^{1,2}	<i>A. africanus</i>
TM 1513	-2.6	.300	Day ¹ ; Vancata ²	<i>A. africanus</i>
ER 3228	-2.0	.461	McHenry ^{1,2}	<i>H. habilis</i>
ER 1472	-1.9	.401	McHenry ^{1,2}	<i>H. habilis</i>
ER 1481	-1.9	.396	McHenry ^{1,2}	<i>H. habilis</i>
OH 62	-1.8	.315	McHenry ^{1,2}	<i>H. habilis</i>
ER 999	-1.7	.410	Day ¹ ; Vancata ²	<i>H. habilis</i>
ER 736	-1.7	.482	McHenry ^{1,2}	<i>H. erectus</i>
ER 1808	-1.7	.485	McHenry ^{1,2}	<i>H. erectus</i>
SK 82	-1.7	.337	McHenry ^{1,2}	<i>H. erectus</i>
ER 737	-1.6	.420	McHenry ^{1,2}	<i>H. erectus</i>
WT 15000G	-1.6	.432	McHenry ^{1,2}	<i>H. erectus</i>
ER 803A	-1.5	.400	McHenry ^{1,2}	<i>H. erectus</i>
OH 34	-1.0	.432	McHenry ^{1,2}	<i>H. erectus</i>
OH 28	-0.7	.456	McHenry ^{1,2}	<i>H. erectus</i>
Trinil 3	-0.6	.455	Day ^{1,2}	<i>H. erectus</i>
Shanidar 1	-0.06	.461	Day ¹ ; Trinkaus ²	<i>H. s. neanderthalensis</i>
Shanidar 4	-0.06	.425	Day ¹ ; Trinkaus ²	<i>H. s. neanderthalensis</i>
Shanidar 5	-0.06	.450	Day ¹ ; Trinkaus ²	<i>H. s. neanderthalensis</i>
Shanidar 6	-0.06	.388	Day ¹ ; Trinkaus ²	<i>H. s. neanderthalensis</i>
Medieval English	-0.001	.444	Robinson ^{1,2}	<i>H. s. sapiens</i>
NA males	0.0	.467	McHenry ^{1,2}	<i>H. s. sapiens</i>
NA females	0.0	.431	McHenry ^{1,2}	<i>H. s. sapiens</i>
Mexican males	0.0	.426	McHenry ^{1,2}	<i>H. s. sapiens</i>
Mexican females	0.0	.380	McHenry ^{1,2}	<i>H. s. sapiens</i>
Japanese	0.0	.399	Robinson ^{1,2}	<i>H. s. sapiens</i>
Australian	0.0	.438	Robinson ^{1,2}	<i>H. s. sapiens</i>
American Negro	0.0	.433	Robinson ^{1,2}	<i>H. s. sapiens</i>
Amerindian	0.0	.450	Lovejoy ^{1,2}	<i>H. s. sapiens</i>

Sources for dates are denoted by (1); those for lengths are denoted by (2). The taxon is that to which the estimator of length assigned the specimen.

L will have a slope close to 1.0. If the gravity-based hypothesis is true, \sqrt{L} will be a better predictor of V_{\max} and a log-log regression of V_{\max} on L will have a slope close to 0.5.

For the fossil study, it is necessary first to show a significant positive correlation between lower limb length (L) and maximum comfortable walking speed (V_{conf}). It is particularly important to show such a relationship with bipedal humans, since a recent study of 21 mammals by Steudel and Beattie (1995) revealed that this is not the case with a number of quadrupeds.

MATERIALS AND METHODS

Subjects

A group of 25 subjects (8 female, 17 male) was recruited to walk and run on a treadmill, in order to determine the maximum possible

walking speed (V_{\max}) of each one. They were instructed to continue walking, as speed was increased manually, until they felt they had to run.

To determine V_{conf} , a group of 23 subjects (10 female, 13 male) was asked to walk and run on a treadmill as speed was increased and decreased by the investigator. They were instructed to walk and run ad libitum (i.e., walk when they felt comfortable walking, and run when they felt comfortable running). Some subjects were experienced with motorized treadmills, while others were not. Those who lacked familiarity with the treadmill were encouraged to use safety features, such as the sturdy handrails which were part of the machine's superstructure and a dead man switch attached to the clothing. All inexperienced subjects were given 5 to 10 minutes to

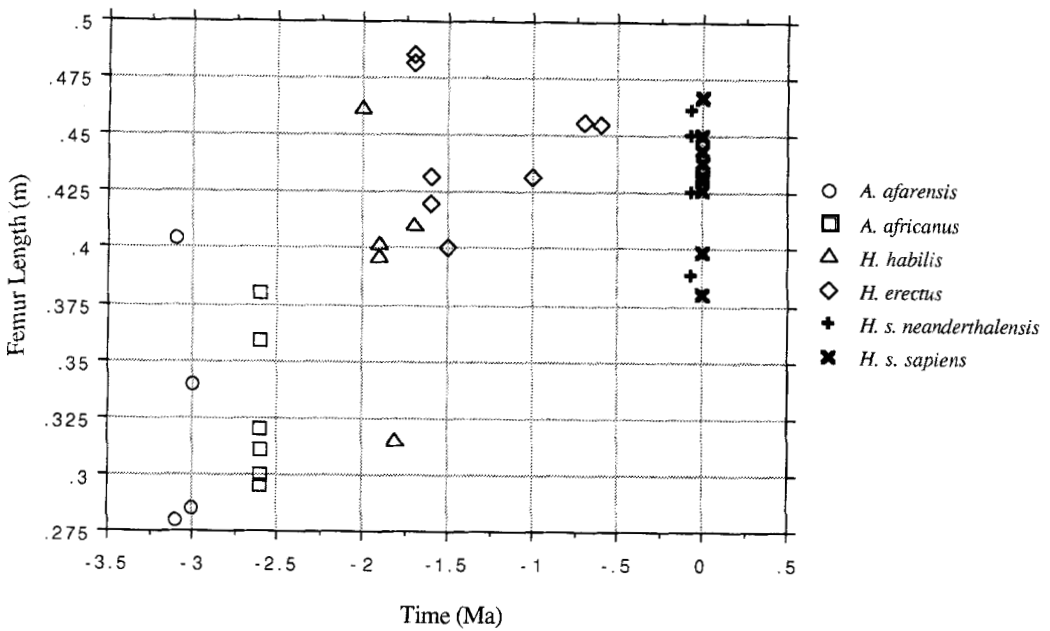


Fig. 3. Femur length vs. time for the hominid specimens listed in Table 1.

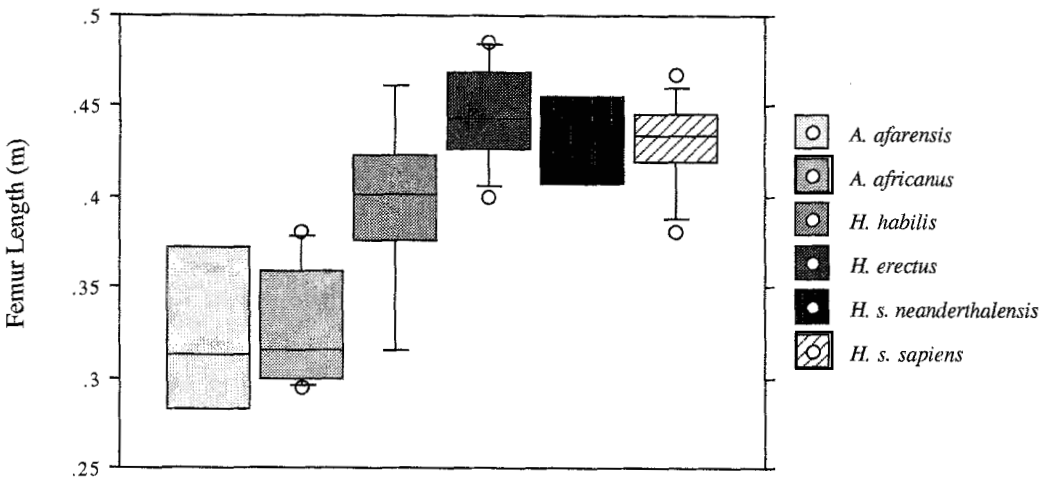


Fig. 4. Percentile box plot of hominid femur length, by taxon. Lines for each box indicate 10th, 25th, 75th and 90th percentiles. Circles indicate outliers not between 10th and 90th percentiles.

become accustomed to the treadmill, and any who were still uncomfortable walking and running without holding the handrails, were subsequently removed from the study. Hence, the total number of subjects for the ad lib trials was eventually reduced to 23. Tables 2 and

3 summarize the basic anthropometric data for the two samples.

Equipment

The treadmill was a Pace Master SX Pro, with sufficient horsepower to ensure that its

TABLE 2. Summary anthropometric data for 25 subjects in main study, in which they were asked to walk as fast as possible, until increasing treadmill speed forced them to run

	Mean	SD	SE	Minimum	Maximum
Age (y)	26.240	6.815	1.363	18	44
Stature (m)	1.768	0.119	0.024	1.534	2.015
Weight (kg)	73.632	21.027	4.205	52.727	135.909
Trochanterion (m)	0.918	0.074	0.015	0.787	1.100

TABLE 3. Summary anthropometric data for 23 subjects in ad libitum trials

	Mean	SD	SE	Minimum	Maximum
Age (y)	27.174	11.171	2.329	19	64
Stature (m)	1.729	0.090	0.019	1.524	1.883
Weight (kg)	76.493	18.107	3.776	45.455	115.455
Trochanterion (m)	0.909	0.066	0.014	0.773	1.027

speed could be increased until it forced the subjects to run, if the researcher desired. The treadmill displayed only miles per hour in increments of $\frac{1}{10}$ mph, so conversion to m/sec was necessary. It was calibrated with a handheld odometer wheel.

A VHS video camera which operates at 30 frames/sec was mounted on a tripod to view the subjects in norma lateralis while the walking trials were being made.

Procedure

After basic anthropometric data, including trochanteric height (L), were collected, each subject was asked to walk and run on the treadmill. Trochanterion was taken as a reasonable estimate of lower limb length, and all measurements were made with clothing and shoes on, since all subjects wore shoes during the walk/run trials. The first group was asked to begin by walking at low speed on the treadmill, and to continue walking as speed was increased, until it became necessary to run (Figs. 5 and 6). Various safety precautions were taken to ensure that the subjects did not injure themselves, especially at high walking speeds. Most subjects were videotaped while walking and running, so that information about their performance could be collected at leisure. The speed at which each subject changed to running was recorded, and the next lowest increment (in $\frac{1}{10}$ mph) was taken as the maximum walking speed (V_{\max}). Results there fore have no resolution of no greater than $\frac{1}{10}$ mph. The speed was recorded on videotape by means of a simple number sign within the field of

view of the camera (Figs. 5 and 6). This sign was adjusted by the researcher to match the speed on the display console of the treadmill. Afterwards, V_{\max} was regressed on L and on \sqrt{L} , and $\log(V_{\max})$ was regressed on $\log L$.

For the ad lib trials, a similar procedure was employed, except that the subjects were told to run or walk, whichever felt more comfortable at any particular speed. Subsequently, V_{conf} was regressed on L.

RESULTS

Maximum walking speed

Figures 7 and 8 show regressions of V_{\max} on L and on \sqrt{L} , respectively. Note the similarity of the r^2 values, both of which indicate that 54% of the variation in the data is explained by the models in each case. Figure 9 shows the log-log regression of V_{\max} on L, and here again, r^2 is 0.54.

Maximum comfortable walking speed

All subjects in the ad lib trials changed from walking to running at speeds between 1.6 and 2.4 m/sec (3.6 and 5.4 mph), with an average of 2.0 m/sec (4.5 mph). Figure 10 shows the regression of V_{conf} on L, with an r^2 value of 0.14 and a slope not significantly different from zero (95% confidence interval is -0.139 to 2.118).

CONCLUSIONS

Maximum walking speed

The results concerning the relationship between V_{\max} and L provide support for the gravity-based hypotheses of Alexander

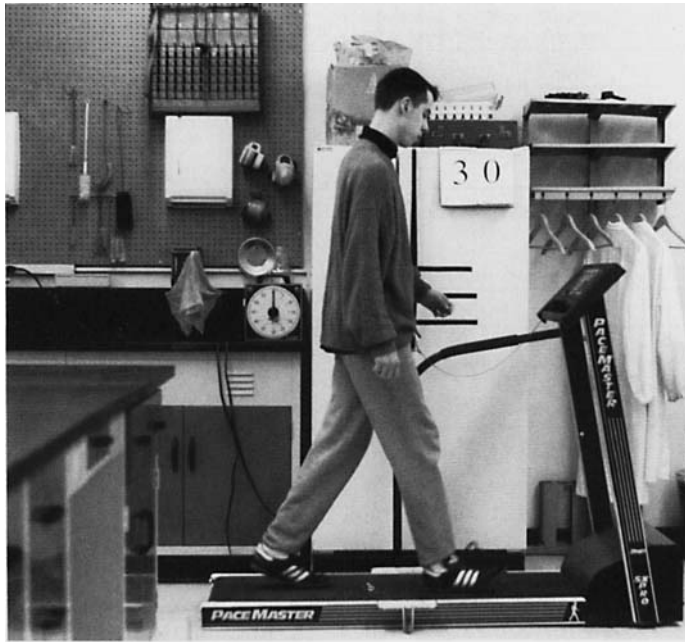


Fig. 5. Subject walking on treadmill. Number sign in upper right indicates speed in $1/10$ mph.

(1984b) and Helene (1984). The slope of the regression line is significantly different from zero ($P < 0.0001$), and the correlation coefficient is 0.733 ($r^2 = 0.54$). The 95% confidence interval for the slope of $\log(V_{\max})$ on $\log(L)$ is 0.401–0.936, which includes the expected slope of 0.5, though it does not include 1.0. Hence, the simplistic null hypothesis, based on intuition and on Garland and Janis' (1993) work, must be rejected, while the gravity-based hypothesis is not rejected. Further support for the gravity-based hypothesis comes from the observation of the following movements which were used variously by the subjects, apparently to increase maximum walking speed:

- thrusting shoulders and arms upward just before mid-stance (counteracts upward motion of the CoM)
- race walking/waddling (reduces vertical displacement of the CoM)
- bending knees (reduces vertical displacement of the CoM)
- shortening stride (reduces vertical displacement of the CoM)
- bending elbows to pump forearm and

hand up and down (counteracts upward motion of the CoM).

Despite the fact that the gravity-based hypothesis fits the data, it is certainly not a perfect fit, and this requires some explanation. The difference between the expected slope of the log-log plot (Fig. 9) and the observed slope is 0.17 (i.e., $0.67 - 0.5$). It is reasonable that the observed slope is higher than the expected, because of the aforementioned "determinants of gait." Saunders et al. (1953) noted six aspects of human bipedalism which alter the path of the CoM from a simple arc, as assumed in this study, to one resembling a sine curve in the sagittal plane. These six determinants are: pelvic rotation; pelvic tilt; knee flexion in stance phase; ankle extension at heel-strike and flexion at toe-off; lateral displacement of the pelvis. All of these determinants reduce the vertical displacement and, hence, acceleration of the CoM, and some of them (e.g., hip rotation) become more pronounced as speed increases towards maximum (Inman et al., 1981; Murray et al., 1966). Therefore, they allow one to attain a higher maximum walk-

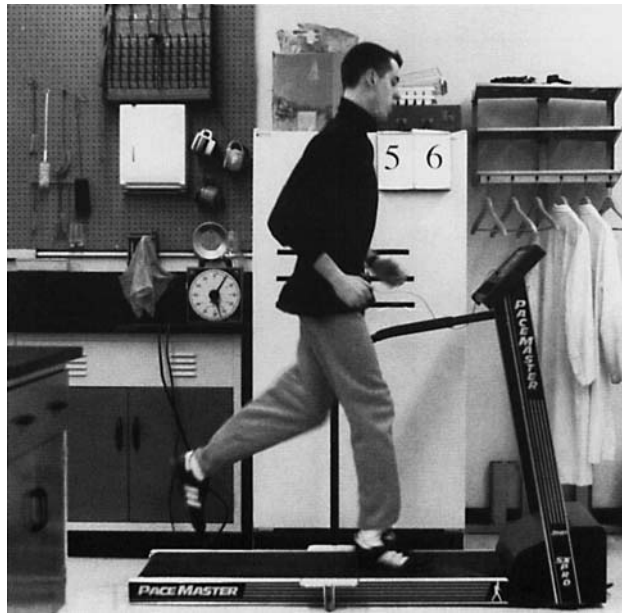


Fig. 6. Subject running on treadmill.

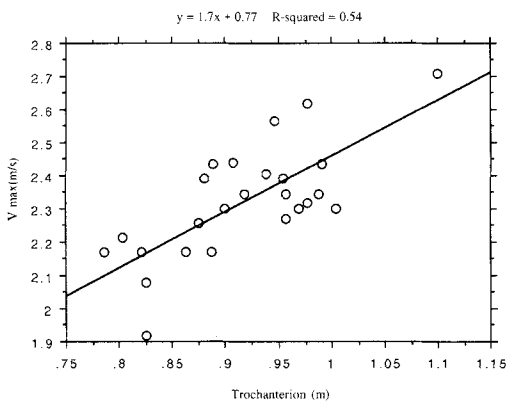


Fig. 7. Regression plot of maximum observed walking speed (V_{\max}) on trochanteric height (L).

ing speed than would be expected under the simple, compass gait model used here.

Maximum comfortable walking speed

The results of this study indicate that maximum comfortable walking speed is not very closely related to lower limb length, a fact that is well-known to amateur and professional runners (B. Coates, pers. comm.).

The slope of the regression line is not significantly different from zero ($P = 0.08$), and the correlation coefficient is only 0.370 ($r^2 = 0.137$). The 95% confidence interval for the slope of V_{comf} on L is -0.139 to 2.118 .

Studies of the transition from walking to running in a variety of non-human animals suggest that energy efficiency, rather than limb length, is the most important factor which determines the speed at which they prefer to begin running (Steudel and Beattie, 1994; Hoyt and Taylor, 1981). It has also been suggested that energetic cost may be the major factor which determines the speed at which humans prefer to begin running (Alexander, 1980; Cavagna and Kaneko, 1977). Furthermore, Steudel (1996) concluded that there is no clear relationship between energetics and limb size, in quadrupeds or hominids, and the results obtained here support her conclusion. However, it may not be possible to explain the transition between gaits on the basis of energetics, either, at least not for humans. For example, work by Hreljac (1993) showed that humans tend to begin running at speeds which are significantly below the point at which run-

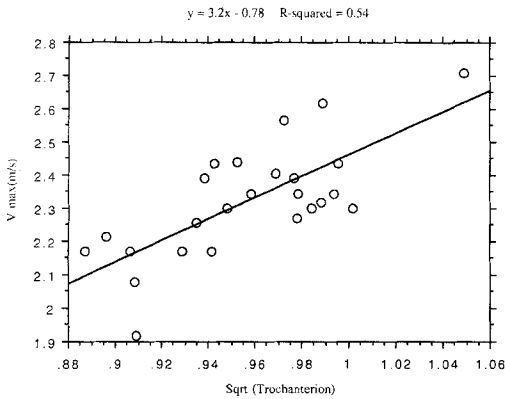


Fig. 8. Regression plot of maximum observed walking speed (V_{\max}) on the square root of trochanteric height (\sqrt{L}).

ning is less expensive than walking. In other words, at speeds approaching V_{comf} (maximum comfortable walking speed), Hreljac's subjects perceived running to be less effort, even though oxygen consumption rates indicated that it was not. Clearly, more work is needed to learn what factors determine V_{comf} .

DISCUSSION

Lower limb evolution in hominids

The trend toward longer lower limbs in hominids, noted by McHenry (1991) and further supported page 520 (Figs. 3 and 4), almost certainly involved an increase in maximum walking speed, at least until ca. 2 Ma BP. However, it is hard to imagine any selective advantage in increased V_{\max} in hominids, especially when high walking speeds could be achieved, with greater efficiency, by running (Cavagna and Kaneko, 1977; Ralston, 1976). It is therefore unlikely that this trend is the result of selection favoring maximum possible walking speed.

Furthermore, greater efficiency at sub-maximal walking speeds does not appear to accrue to those with longer lower limbs. This is evidenced by the fact that V_{comf} was not closely related to L , in the experiment performed here. We must conclude therefore (as did Steudel, 1996) that increased L was not the result of selection pressure for increased efficiency in walking. Therefore, other explanations must be sought. Garland and Janis

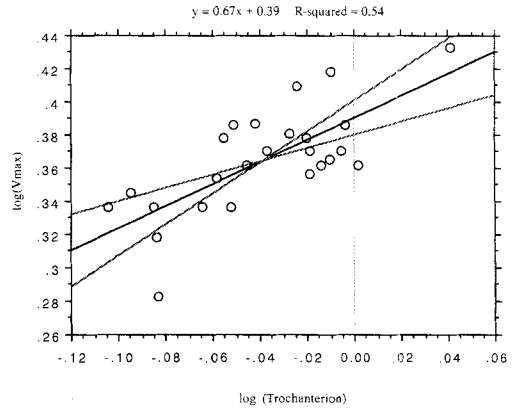


Fig. 9. Log of maximum observed walking speed regressed on the log of trochanteric height. Dotted lines indicate 95% confidence interval for the slope of the regression line (0.401-0.936).

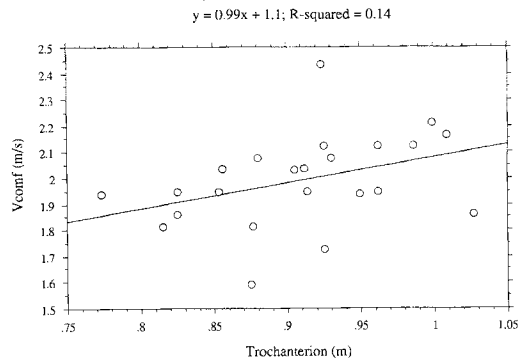


Fig. 10. Regression plot of maximum comfortable walking speed (V_{comf}) on trochanteric height (L).

(1993) noted an association between femur length and maximum running speed in quadrupeds, and this may well be true of bipedal hominids, also. If so, then maximum running speed probably increased in early hominids from about 4 Ma BP to 2 Ma BP. A test of lower limb length vs. maximum running speed in modern humans might help determine the validity of this argument, but there are certain to be confounding factors in such a test. For example, professional basketball players are generally not world class sprinters, so the difficulties of moving long limbs rapidly must be investigated. Also, muscle fiber type may be a much more

important factor than limb length in determining maximum running speed. If maximum running speed was selected for, it was most likely not for chasing prey (as suggested by Dart, 1926; 1971), but perhaps for avoiding predators (as suggested by the work of Brain, 1981). Indeed, the evolution of longer lower limbs in early hominids may not have been for locomotor purposes at all. Perhaps Ruff's (1994) explanation regarding temperature adaptation and Allen's Rule is more relevant. In any case, the results of this study suggest that longer lower limbs may be a boon to modern race walkers, but would not have been very beneficial for early hominids' walking.

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